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Beta-diversity on deep-sea wood falls reflects gradients in energy availability

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Wood falls on the deep-sea floor represent a significant source of energy into the food-limited deep sea. Unique communities of primarily wood- and sulfide-obligate species form on these wood falls. However, little is known regarding patterns and drivers of variation in the composition of wood fall communities through space and time, and thus, how wood falls contribute to deep-sea biodiversity. Eighteen *Acacia* logs varying in size were placed and retrieved after five years at a 3200 m site in the Pacific Ocean. We found that the taxonomic composition and structure of deep-sea wood fall communities varied considerably and equated with considerable differences in energy usage and availability. Our findings suggest that natural variability in wood falls may contribute significantly to deep-sea diversity.

1. Introduction

Wood transported to the oceans via rivers eventually becomes saturated with seawater and sinks to the ocean floor. The total input of this wood debris and associated carbon to the oceans is sizeable and pervasive, even to abyssal depths [1]. During the Typhoon Morakot in 2009, a total of 8.4×10^9 kg of woody debris was transported to the oceans off Asia [2]. However, the amount of wood arriving to the deep oceans may be changing owing to deforestation [3,4] and increasing river discharge [5].

Once on the deep-sea floor, wood falls form unique communities composed primarily of wood and sulfide obligate species. Wood falls thus represent oases on the typically food-limited deep-sea floor. Energy is transferred from wood to associated animals via both heterotrophic and chemotrophic pathways. Heterotrophic, cellulose-degrading microflora such as bacteria and fungi are also fed upon by other organisms [6,7]. Some animals may also digest and assimilate carbon from wood directly [6,8]. The most notable and abundant are members of the wood-boring bivalve subfamily Xylophagainae [9–14], keystone species that radically shape wood fall communities [10]. Wood chips and faecal pellets produced by xylophagainids promote growth of chemautotrophic and cellulose-degrading bacteria, which in turn make wood energy available to animals that are not wood obligates [15]. In addition, anaerobic breakdown of wood by sulfate-reducing bacteria also produces sulfide leading to a chemotrophic energy pathway. Biochemical oxidation of sulfide can fuel carbon fixation by chemolithoautotrophic microbes, which are then consumed by other organisms [15,16].

Most research on wood fall communities has focused on the formal description of species colonizing wood falls and the potential for wood falls to serve as stepping stones between chemosynthetic communities [9,12,15–18]. Little is known concerning patterns of variation in the composition of biological assemblages associated with wood falls over space and time, and thus, how wood falls contribute to deep-sea biodiversity. Here, we demonstrate that wood fall communities can vary greatly as both a function of wood fall size and successional state, two different dimensions of energy availability in these communities. Our results show that community composition at wood falls can

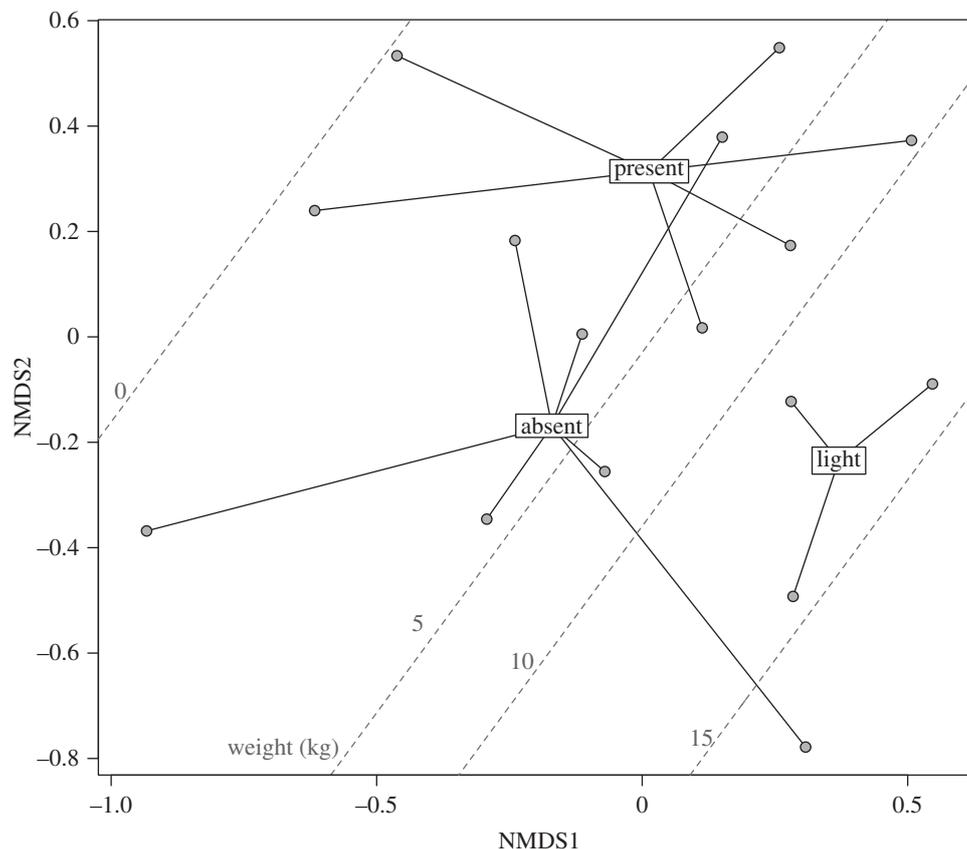


Figure 1. Non-metric multidimensional scaling plot based on arcsine transformed abundances for wood fall communities. Grey filled circles denote individual wood falls. Dashed lines indicate direction of change in log size (small top left to large bottom right). Wood falls are linked together by the presence of a halo on the surrounding sediment (absent, light, present).

also vary considerably over small geographical distances, suggesting a potentially substantial contribution to the development and maintenance of deep-sea diversity.

2. Material and methods

In November 2006, 36 pieces of *Acacia* logs were deployed at 3203 m in the Northeast Pacific Ocean (Station Deadwood: 36.154098° N, 122.40852° W). The *Acacia* logs ranged in size from 0.6 to 20.6 kg. Logs of various shapes were chosen to reduce the correlation between surface area and weight. The logs were deployed in a randomized block design over an approximately 500 m² area. Each log was sewn into a synthetic fibre mesh bag (5 mm mesh). Eighteen *Acacia* logs were collected in October 2011 (five years). Logs were placed into 300 µm mesh bags with sealable closing lids during ROV retrieval, ensuring no loss of individuals and/or cross contamination among different samples. All specimens were picked from wood, preserved and later identified to the lowest possible taxonomic level. For each wood fall, we recorded the initial weight, location, surface area and successional stage. Additionally, the experimental site was observed annually and HD video taken of each wood fall. This allowed successional stage to be identified by the presence or the absence of a 'halo' on the sediment around the wood fall. The occurrence of these 'halos' result from the wood chips and fecal pellets produced by Xylophaginae which, in turn, promote the growth of cellulose-degrading microflora and chemolithoautotrophic bacteria in a ring around the wood fall itself. These halos of activity are easily observed in video as an area of discoloration compared to the surrounding sediments and represent a high biomass/energy successional stage. Species and wood fall data are available at <http://datadryad.org/resource/doi:10.5061/dryad.8j013>.

Multivariate analyses were conducted in the R using the Vegan package [19]. Bray–Curtis similarities were computed on the arcsine transformed abundances, and an MDS was conducted to visualize differences in community structure. A constrained analysis of principal coordinates (CAP) analysis, related to a redundancy analysis but allowing for non-Euclidean distances like Bray–Curtis, was used to analyse the effect of wood weight, surface area, location and successional state (i.e. presence of a halo). Complete R scripts for the analyses are available at <http://datadryad.org/resource/doi:10.5061/dryad.8j013>.

3. Results

The dissimilarity in wood fall communities ranged from 21.9 to 99.6% (mean = 74.7%). A CAP model including wood mass, surface area, successional state and location within the sample area revealed only mass and successional state as significant predictors of community structure ($p = 0.0179$ and 0.0231 , respectively). A Mantel test also confirmed that geographical distance between wood falls was unrelated to differences in their community structure ($p = 0.064$, $r = 0.1282$). Wood mass and successional state explained 45.2% of the variance in community structure among individual wood falls (figure 1). The CAP analysis indicated that differences in community structure due to wood mass were primarily associated with the abundances of three gastropods (*Xyloskenia* sp. nov., *Hyalogyra* sp. 1 and *Provanna* sp. 1; figure 2).

The main indicator species of successional stage, besides the wood-boring bivalve *Xylophaga zierenbergi* were a tanaid crustacean, *Protanais* sp. nov. and a Polynoidae polychaete. Annual video observations of the wood fall communities

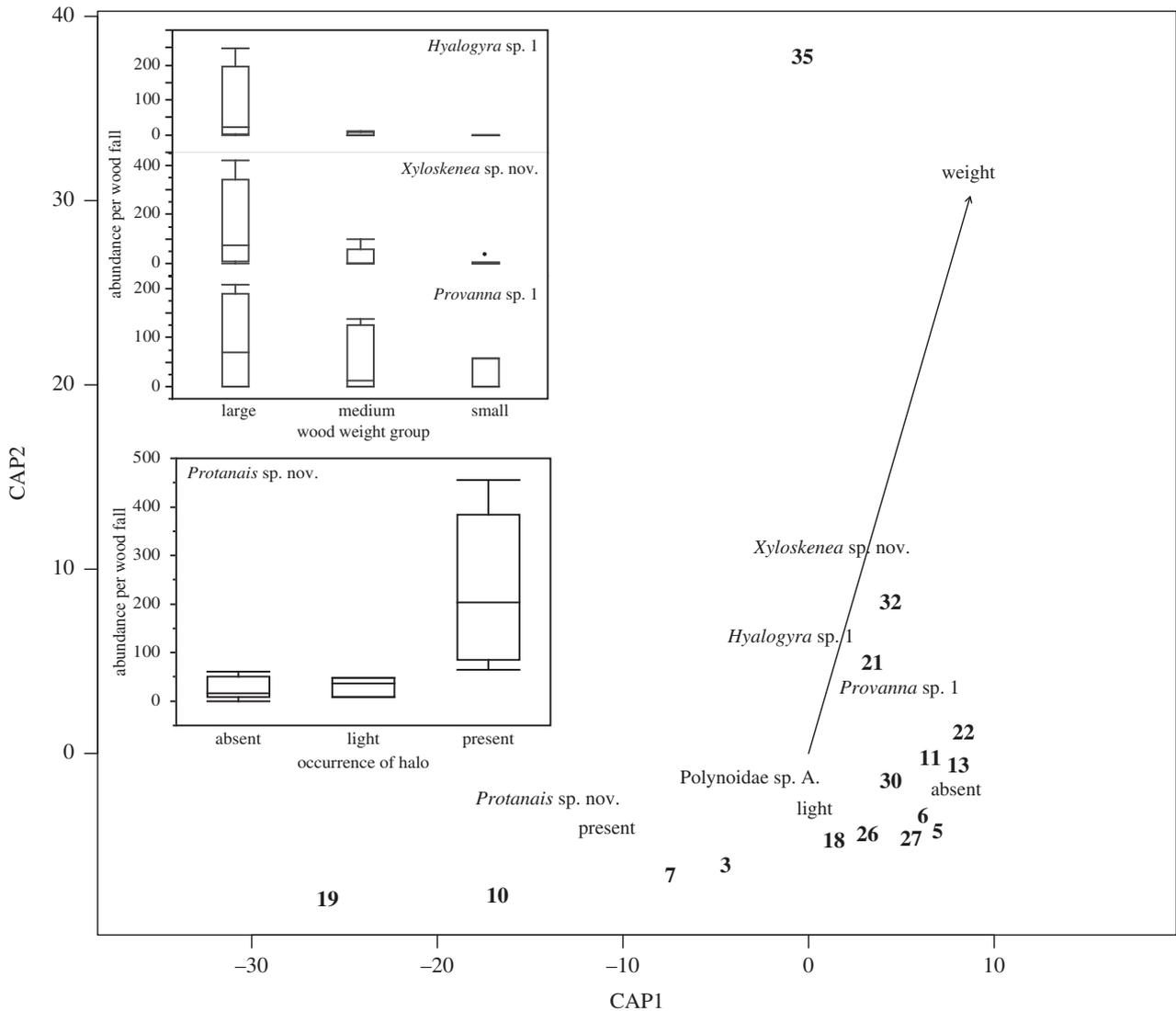


Figure 2. Constrained analysis of principal coordinates (CAP) plot. Numbers denote individual wood falls. Location of species names, halo labels and weight indicates strength and direction of that factor on the wood fall community in multivariate space. Inset of box plots indicate changes in abundances of species over different wood fall ages or sizes.

indicated that despite the identical deployment time, colonization and development of wood fall communities varied greatly. At five years, some wood falls still contained numerous actively boring *X. zierenbergi*, corroborated by the presence of a characteristic 'halo' around these wood falls.

4. Discussion

Here, we demonstrate that the taxonomic composition and structure of deep-sea wood fall communities varied dramatically and equated with considerable differences in energy usage and availability. Early colonizers of wood include wood-boring bivalves of Xylophaginae [11,15]. These Xylophaginae serve as ecosystem engineers of wood falls; their boreholes generate space for inhabitation by other species and serve as prey for predators [11]. Xylophaginae also litter the wood fall and surrounding sediment with wood chips and faeces, providing usable sources of carbon [20]. The enhanced respiration from increased biomass at this stage also leads to the development of sulfidic niches that attract animals that rely nutritionally on chemolithoautotrophic bacteria [15]. The main indicator species of

successional stage, driven by the wood boring of *Xylophaga zierenbergi* [13], was a new tanaid species of the genus *Protanais*. This species may be a predator on *X. zierenbergi* or perhaps feeds on the faecal pellets and associated bacteria of *X. zierenbergi* [21].

Our results suggest that succession in wood fall communities can be considerably slower and more stochastic than previously believed [15]. At five years, some wood falls contained numerous actively boring *X. zierenbergi*. By contrast, other wood falls had low abundances and small sizes of *X. zierenbergi* suggesting more recent colonization. Our use of *Acacia*, a hardwood, as opposed to soft woods typically used in other studies, may account for some of the variation in observed rates of community development. A hardwood may reduce rates of colonization and boring by *X. zierenbergi*, leading to slower changes in community structure and slower rates of energy delivery to other constituents of the wood fall community. Growth of *Xylophaga* is known to differ between oak and pine panels [22]. In contrast to the oak and pine, teak on the *Titantic* appeared to be relatively unbored by bivalves even after 70 years [23]. This suggests that wood density may contribute significantly to the beta-diversity of wood fall assemblages by regulating rates of energy delivery to the community via the Xylophaginae pathway.

The sizes of individual logs also led to considerable variation among experimental wood fall communities. Log mass significantly predicted variation in community structure; by contrast, the surface area of logs was repeatedly eliminated from best-fit models. This suggests that variation in community structure may be unrelated to surface area available for larval recruitment. Alternatively, larger, more massive wood falls provide more energy, thereby promoting a greater assortment of niches. In addition, larger wood falls may allow for greater population sizes overcoming potential Allee effects in some species. Indeed, larger wood falls were characterized by the presence of three gastropod species, including two that graze on bacterial films from hard substrata. Deep-sea molluscs have been shown previously to be sensitive to gradients in energy availability over larger spatial scales and prone to Allee effects at lower food availability [24,25].

Patterns of beta-diversity of wood fall communities, as observed for other deep-sea systems [26], appear to be driven primarily by energy availability. Successional stage denoted the presence/absence of an ecosystem engineer that made energy accessible to other species. Prior work has shown that this wood fall-derived energy also greatly affects the

community structure of the nearby sediment [20]. Wood fall mass described the total energy available to the community. These different energetic dimensions predicted approximately 45% of the variation in community structure among logs. The composition of wood fall communities also appears to be highly stochastic. Communities observed at 18 logs deployed in close proximity (less than 500 m²) for five years were on average nearly 75% dissimilar. This apparently high beta-diversity among wood falls may derive from small-scale variation in recruitment, unknown variation in suitability among logs or other unidentified processes. Overall, our findings suggest that natural variability in wood falls may contribute significantly to deep-sea diversity.

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Data accessibility. Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.8j013>.

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